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Scales and symmetries of eco-evo: advective environments, dispersal, and climate change

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Running headline: Dimensions of eco-evo.

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Abstract

I investigate effects of directional advective dispersal on eco-evolutionary invasion speeds, in either constant environmental gradients or under directional environmental change. I build upon a spatially-explicit phenotypic model that I have previously presented. The model incorporates both phenotypic sorting and gene swamping, and is used to study either constant advective dispersal or trait-based habitat choice. Through analytical arguments on characteristic lengths and speeds, as well as by direct numerical solutions, I find that, in eco-evo scenarios, advective dispersal has two opposing effects on pulled invasion fronts. In shallow environmental gradients, the demographic effect of simply adding to the steady-state invasion speed dominates. As gradients get steeper, asymmetric gene flow, due to advective dispersal, becomes increasingly stronger, pulling the invasion front in an opposite direction. Steep gradients cause front reversals, where species ranges, counter-intuitively, slide upstream. Symmetry between velocity of advective dispersal and velocity of climate change leads to adaptation lags, abundance profiles, and invasion speeds that depend only on the velocity difference. Through characteristic lengths and speeds, I also identify a symmetry between demographic and evolutionary averaging or tracking of environmental heterogeneity. I connect climate change research to demographic models of persistence in advective environments — the so-called drift paradox. I additionally derive several dimensionless ratios that have potential in facilitating comparisons among different species, traits and locales, and in guiding micro- and mesocosm experiments and space-for-time substitutions. As an aside, I demonstrate how numerical solution and simulation of complex eco-evo models can be accelerated with GPU programming.

Keywords: advective dispersal, directional dispersal, gene swamping, range expansion, biological invasion, spatial sorting, matching habitat choice, evolutionary invasion speed, characteristic length, critical domain size

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Introduction

There is an inherent symmetry between the velocity of climate change and the directional dispersal or flow that organisms experience in advective environments, such as rivers, propagule-carrying ocean currents and seed-dispersing winds. Though lost now in the older strata of an ever more recent literature, earlier theoretical work on population persistence under climate change (Potapov & Lewis 2004, Berestycki et al. 2009) originated in such persistence models for advective environments, namely, on the so-called drift paradox (Speirs & Gurney 2001, Anderson et al. 2005, Pachepsky et al. 2005, Lutscher et al. 2006, Nisbet et al. 2010, Vasilyeva & Lutscher 2012). In fact, when solving for conditions of persistence under climate change Potapov & Lewis (2004) applied the argument of "habitat motion as advection of biota" and, accordingly, transformed the initial climate-change formulation into a model of an advective environment.

There has also been much renewed interest in similar classic reaction-diffusion models of biological invasions (Skellam 1951, Shigesada & Kawasaki 1997, Murray 2002). Especially by recent studies that apply swarming microbes (Ben-Jacob et al. 1998) as microcosm models for eco-evolutionary (hereafter, *eco-evo*) dynamics of adaptation and range expansion (Gandhi et al. 2016, Deforet et al. 2017, Birzu et al. 2019, Erm & Phillips 2020).

Eighteen years ago (Filin 2007), I presented a phenotypic reaction-advection-diffusion (also reaction-transport; Ishihara et al. 2020) eco-evo model that combined gene swamping (Pease et al. 1989, Kirkpatrick & Barton 1997, Lenormand 2002), spatial sorting (Shine et al. 2011) and matching habitat choice (Edelaar et al. 2008), though the latter two terms were not yet invented. I then provided a systematic exploration of different forms of *advective dispersal* (also, directional, asymmetric, nonrandom, anisotropic, directed, biased, unidirectional or drift; Gurney & Nisbet 1975, Nagylaki 1978, van den Bosch et al. 1990, Levine 2003, Filin 2007, Nisbet et al. 2010, Sorte 2013, Hancock et al. 2024), and how they affect eco-evo dynamics and range expansions. Here, I recap and elaborate on my approach and some of my results, present them within current eco-evo context, and provide new analyses, to demonstrate

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how the study of advective dispersal highlights the nuances of eco-evo dynamics.

Two classic results of spatially-explicit reaction-diffusion population models in ecology are critical domain (or patch) size and constant steady-state invasion speed (Skellam 1951, Kierstead & Slobodkin 1953, Okubo 1984, Shigesada & Kawasaki 1997, Potapov & Lewis 2004, Nisbet et al. 2010). Critical domain size defines a demographic characteristic length, over which spatial variation in population (per-capita) growth (e.g., spatial variation in recruitment; Nisbet et al. 2010) is averaged. A population may not be able to persist in an otherwise favorable source patch, if surrounding sinks dominate in this spatial averaging. In other words, critical domain size defines the finest spatial resolution of habitat heterogeneity, to which populations can respond, shifting from averaging spatial heterogeneity to tracking it (Roughgarden 1974, Anderson et al. 2005, Nisbet et al. 2010). When random dispersal is denoted by a diffusion coefficient, D, and per-capita growth rate by r, the critical patch size is proportional to $\sqrt{D/r}$ (Kierstead & Slobodkin 1953, Nisbet et al. 2010).

In invasion scenarios, the quantity $\sqrt{D/r}$ also defines the shape of the advancing front, i.e., the spillover or decay of population density with distance (Gandhi et al. 2016). The speed at which this invasion front propagates, through population growth and random dispersal, is $c_0 = 2\sqrt{rD}$ (Skellam 1951, Shigesada & Kawasaki 1997). This is the steady-state invasion speed of pulled waves (Birzu et al. 2019), if Allee effects do not play a significant role in the demographic dynamics. I will refer to c_0 as the *Fisher velocity* (also, Fisher wave speed; Fisher 1937, Nisbet et al. 2010, Gandhi et al. 2016, Birzu et al. 2019). It is a baseline invasion wave speed for homogeneous environments, negatively density-dependent growth (i.e., no Allee effect), and only random dispersal.

In eco-evo models, however, evolutionary dynamics, such as of the mean phenotype or trait distribution across space, also introduces characteristic dimensions of its own. Specifically, for mean trait, the evolutionary characteristic length, hereafter *characteristic length*, is given by $L = \sqrt{D/sG}$ (May et al. 1975, Endler 1977, Slatkin 1978, Lande 1982b, 1991, Barton 1999, Kruuk et al. 1999, Day 2000, Filin 2007), where s is a measure of the strength of stabilizing selection towards a spatially varying local optimum, and G is the trait's additive genetic

variance within local populations (Methods). As the ecological critical patch size, the characteristic length defines averaging by random dispersal of spatially varying selection (Lande 1982b). Consequently, local mean phenotype is a weighted average of spatially varying optima, determined by an averaging kernel that decays with distance according to L (Slatkin 1978, Lande 1982b, Filin 2007).

There is also an evolutionary characteristic speed, analogous to c_0 of demographic invasion dynamics, $c_g = 2\sqrt{DsG}$ (clearly related to Fisher's 1937 original formulation for spread of advantageous mutations; compare also with the critical speed of Kirkpatrick & Peischl 2013, for evolutionary rescue in single-locus models). I will refer to it here as the *characteristic speed*. In the context of this work, this measure does not describe spatial spread *per se*. But, rather, it defines a speed scale, by which other velocities are weighed to influence mean trait values.

Of course, the heart of eco-evo is the coupling of the two types of dynamics — demographic and evolutionary. Evolution affects demography via local maladaptation, deviation of mean trait from local optimum, which depresses mean fitness and per-capita growth (Kirkpatrick & Barton 1997, García-Ramos & Rodriguez 2002, Barton 2024). In the opposite direction, the effect of demography on evolution is, traditionally, through mixing by random dispersal (or migration), and through gene swamping — the tendency of the mean trait to deviate from the local optimum towards optima of more populous localities, due to the relatively stronger incoming gene flow from those localities (Pease et al. 1989, Kirkpatrick & Barton 1997, Lenormand 2002). Gene swamping, therefore, distorts the evolutionary averaging kernel, extending it upstream, while contracting downstream (Slatkin 1978, Filin 2007).

From a modeling perspective, gene swamping introduces a directional *advection* term to the evolutionary dynamics (asymmetric gene flow), while no advection is present in the demographic dynamics, if dispersal is random and symmetric. In purely demographic models, directional advective dispersal, denoted by advection velocity u, adds to the rate of range expansion, resulting in a combined invasion speed, $c = c_0 + u$ (van den Bosch et al. 1990, Shigesada & Kawasaki 1997). Advection velocity also affects conditions for persistence of

populations in such advective environments as rivers and streams, wind- and waterborne seed dispersal, or larval dispersal of marine invertebrates — the so-called drift paradox (Speirs & Gurney 2001; drift in the sense of advective flow). Conditions for persistence depend on velocity of advective dispersal, in conjunction with the critical domain size, $\sqrt{D/r}$, and the Fisher velocity, c_0 (Speirs & Gurney 2001, Anderson et al. 2005, Nisbet et al. 2010). The motivation of my investigation is to explore how such advective dispersal also modulates the feedback between demography and evolution in eco-evo scenarios, to affect characteristic lengths, invasion speeds and possible range pinning, in either constant environmental gradients or under directional environmental change.

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Methods

The notation I adopt here is common in physics and theoretical ecology (Gurney & Nisbet 1975, Shigesada & Kawasaki 1997, Okubo & Levin 2001, Ishihara et al. 2020). Somewhat different notation is used in population genetic models (Pease et al. 1989, Kirkpatrick & Barton 1997, García-Ramos & Rodriguez 2002, Polechová et al. 2009). In the SI, I provide a brief guide for the perplexed on notation.

I follow Filin (2007) in considering a general spatially-explicit phenotypic reaction-advection-diffusion model for population density, $n(\boldsymbol{x})$, and frequency distribution of trait values within local populations, $f(z, \boldsymbol{x})$. In reaction-advection-diffusion population models, random dispersal is denoted by a diffusion coefficient, D, and a directional component of dispersal is denoted by an advection velocity vector $\boldsymbol{u}$. In general, both components of dispersal can depend on space, $\boldsymbol{x}$, time, t, trait or phenotypic value, z, and population density, n. In its most general form (Filin 2007; Appendix), there is an "effective fitness" term that combines relative fitness, $W - \bar{W}$, relative random dispersal ability, $D - \bar{D}$, and relative advective dispersal, $u - \bar{u}$, demonstrating the equivalence of selection and spatial sorting (Shine et al. 2011, Phillips & Perkins 2019) and providing a quantitative expression for assessing their relative strengths in different eco-evolutionary scenarios.

At this point, I make the simplifying assumptions of one-dimensional space, $\boldsymbol{x} = x$ (dropping the vector notation), of normal phenotypic distribution with mean $\bar{z}$ and a fixed variance, of logistic density-dependence, of stabilizing selection towards a spatially and temporally varying optimum, $\theta(x)$ (Slatkin 1978, Lande 1982b, Pease et al. 1989, Kirkpatrick & Barton 1997), such that fitness is given by $W(n, z) = rn(1 - n) - \frac{1}{2}s(z - \theta(x, t))^2$ (where, without loss of generality, population density is scaled such that carrying capacity is 1), and of fixed random dispersal ability, $D = const$. In addition, I replace the relative fitness term, $W - \bar{W}$, in the dynamics the of mean phenotype with Lande's (1976) approximation under weak selection (see Appendix), which introduces the additive genetic variance, G, into the dynamics of $\bar{z}$. Here, I only consider fixed additive genetic variance, $G = const$ (but see

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Discussion).

The simplest form of advective dispersal is a fixed velocity, $u = const$. It can be interpreted as the effect of a prevailing wind direction, flow in a river, or as asymmetry in the spatial distribution of dispersers or propagules (asymmetric dispersal kernels; Slatkin 1978, Okubo & Levin 1989, Levine 2003). Similarly, directional temporal environmental change, hereafter *climate change*, can be described by a linearly time-varying environmental gradient, given by $\theta(x,t) = b(x - u_\theta t)$, where u_θ is the velocity of climate change (Pease et al. 1989, Loarie et al. 2009). The parameter b represents the slope of the environmental gradient, measuring how steeply selective forces vary across space (Kirkpatrick & Barton 1997, García-Ramos & Rodriguez 2002). (This notation is completely equivalent to $\theta = bx - kt$ of Bürger & Lynch 1995, Lande & Shannon 1996 and Polechová et al. 2009, where k denotes temporal rate of change in local conditions; $k = bu_\theta$.)

Given constant advective dispersal, eco-evo dynamics of population density, $n(x,t)$, and local (mal)adaptation, $a(x,t) = \bar{z}(x,t) - \theta(x,t)$, are given by

$$\frac{\partial n}{\partial t} = D\nabla^2 n - u\nabla n + \left[r(1-n) - \frac{1}{2}sa^2\right] n, \qquad [1]$$

$$\frac{\partial a}{\partial t} = D\nabla^2 a - sGa + bu_\theta + 2(b + \nabla a)D\Phi, \qquad [2]$$

where ∇ denotes spatial derivative (in this case of one-dimensional space, $\nabla = \frac{\partial}{\partial x}$). The parameter Φ represents gene swamping, i.e., gene flow asymmetry. In this case, it combines the effect of directional advective dispersal with the traditional effect of population density gradients,

$$\Phi = \frac{\nabla n}{n} - \frac{u}{2D}. \qquad [3]$$

I will refer from now on to the direction opposite to u as *upstream*, and the direction of u as *downstream* (Levine 2003, Sorte 2013). (The above two dynamics equations are, up to differences in notation [see SI] and the extra advection terms, the same as previously presented for eco-evo dynamics along environmental gradients; Pease et al. 1989, Kirkpatrick & Barton 1997, Case & Taper 2000, García-Ramos & Rodriguez 2002, Polechová et al. 2009.)

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Beyond a fixed dispersal bias, there are many forms that can be explored. Here, I only present phenotype-dependent (matching) habitat choice (Filin 2007, Edelaar et al. 2008). (Additional forms were explored in Filin 2007.) In an analogous manner to evolving populations climbing up fitness gradients in (multivariate) trait space (Lande 1982a), matching habitat choice can be viewed as advective dispersal up spatial fitness gradients, $u = \chi \boldsymbol{\nabla} W$ (Filin 2007). The proportionality coefficient, χ, was adopted from models for chemotaxis (Keller & Segel 1971), where it is called chemotactic mobility and measures the sensitivity of movements of cells to concentration gradients of nutrients. In the context of habitat choice, this parameter translates fitness differences among neighboring environments to rates of advective dispersal, u. It has dimensions of length squared. Therefore, χb^2 has dimensions of trait variance.

Given the above fitness function, describing stabilizing selection, mean advective dispersal, $\bar{u}$, and relative advective dispersal, $u - \bar{u}$, under habitat choice, are

$$\bar{u} = \chi a(x,t) s b = \chi(\bar{z} - \theta) s b, \qquad [4]$$

$$u - \bar{u} = \chi(z - \bar{z}) s b. \qquad [5]$$

These can be substituted in the general equations of eco-evo dynamics (for n and f; Eq.[9] and Eq.[10] in Appendix), to produce modified expressions for $\frac{\partial n}{\partial t}$ and $\frac{\partial a}{\partial t}$ (in Appendix).

Finally, numerical solutions of the eco-evo equations for $n(x,t)$ and $a(x,t)$ were implemented with GPGPU — general purpose computing on graphics processing units — and run on a personal laptop computer. Programming was done in JavaScript, WebGL and GLSL (OpenGL shader language). This allowed me to write, compile and run programs on the vastly parallel GPU, and to utilize and access GPU memory (video memory) directly. Such hardware acceleration of numerical procedures allowed for quick software development iterations and wide exploration of parameter space. I used the classic explicit finite-difference method for parabolic equations (Smith 1985), which, although lacking in sophistication, easily lends itself to parallelization on GPUs. As in Filin (2007), I numerically solved for log-transformed population densities, $\ln(n)$, rather than n directly. More details on numerical procedures in SI.

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Results

With advective dispersal at velocity u, an equilibrium solution of uniform population density across the entire environmental gradient is characterized by a constant level of local maladaptation, $a = -ub/sG$. This expression is the mirror image of the lag in adaptation due to climate change at velocity u_θ (Lande & Shannon 1996, Polechová et al. 2009), resulting in the combined expression

$$a = \frac{(u_\theta - u)b}{sG}. \qquad [6]$$

This symmetry between velocity of climate change, u_θ and velocity of advective dispersal, u, suggests a possible interesting direction for space-time substitutions (Lovell et al. 2023) in climate change research. Namely, studying populations that have historically adapted under conditions of advective dispersal (Sorte 2013), as an analogy for future adaptation (or failure to adapt) under climate change. It also points at advective dispersal as a possible adaptive reaction to negative effects of directional environmental change, as demonstrated in Fig. 1E,F. That can be grasped intuitively because, as optimal environments shift downstream (e.g., poleward), advective dispersal helps to restore a match between incoming dispersers and local environment.

Symmetry is also evident when exploring so-called evolutionary speeds of species invasions (García-Ramos & Rodriguez 2002, Filin et al. 2008). For shallow environmental gradients (small b), an approximate expression for invasion speed, c, relative to velocity of climate change, u_θ, is

$$c - u_\theta = \frac{\sqrt{c_0^2 - Q^2(u-u_\theta)^2} + (u - u_\theta)}{1+Q^2}, \quad Q = \sqrt{\frac{2Db^2}{sG^2}} \propto \frac{bL}{\sqrt{G}}, \qquad [7]$$

combining random dispersal (D), advective dispersal (u), velocity of climate change (u_θ) and effects of environmental heterogeneity (b) (see Appendix for derivation). This relative invasion speed clearly depends, as in Eq.[6], only on the difference $u - u_\theta$. The dimensionless quantity Q is the change in environmental conditions (optimum trait value) over a characteristic length, measured in additive genetic standard deviations. In homogeneous environments ($b = Q = 0$), Eq.[7] becomes the purely demographic invasion speed $c_0 + u$. For no climate change and no

advective dispersal ($u = u_\theta = 0$), Eq.[7] reduces to a previously presented expression for "critical speed" (Miller 2019).

A systematic computational exploration, from shallow to steep environmental gradients, reveals that, as gradients get steeper, there can be reversal of range expansion, causing slowly expanding and pinned ranges (Kirkpatrick & Barton 1997) to slide, counter-intuitively, in an opposite direction to the velocity of advective dispersal. This can be understood by considering the balance of forces operating on range expansion in eco-evo scenarios. Demographic invasion models show that (with no Allee effect) invasion wave fronts are pulled forward (Gandhi et al. 2016) by population growth and dispersal at the advancing front. However, in eco-evo models there is another kind of pulling, operating in an opposite direction, namely, gene swamping. Because of asymmetric gene flow, caused by density gradients (Eq.[3]), the evolutionary averaging kernel is asymmetric and biased upstream, thus pulling the mean phenotype at the advancing front away from local optima. This upstream pulling induces maladaptation and reduces population growth at the advancing front. Directional advective dispersal, $u > 0$, adds to this upstream pulling, as Eq.[3] demonstrates.

The effect of advective dispersal on invasion speed, is, therefore, on the one hand, to add to the downstream invasion speed — the purely demographic effect, $c = c_0 + u$ (Shigesada & Kawasaki 1997). On the other hand, advective dispersal increases the upstream pull of gene swamping, dragging the species range in an opposite direction. The balance of these opposing forces is dependent on the steepness of the environmental gradient, b (Fig. 1), and on the magnitude of upstream pulling by gene swamping. This upstream pulling is measured by a dimensionless quantity of gene flow asymmetry,

$$\varphi = \Phi L = L \nabla \ln n - \frac{u - u_\theta}{c_g} \qquad [8]$$

(Appendix). (For uniform population densities, $\nabla \ln n = 0$, and no climate change, $u_\theta = 0$, this expression is equivalent to the asymmetry parameter of May et al. 1975, and to $\tilde{m}$ of Nagylaki 1978, for single-locus allele-frequency clines.)

For uniform population density this expression is simply $(u_\theta - u)/c_g$. For population

densities that decrease exponentially with distance, $n \propto e^{-x/\lambda}$ (as in purely demographic invasion fronts; Murray 2002; λ representing decay length; Gandhi et al. 2016, Deforet et al. 2017), gene flow asymmetry is given by $\varphi = -L/\lambda - (u - u_\theta)/c_g$, namely, the relative drop in population density over a characteristic length minus the advective dispersal velocity, relative to velocity of climate change, scaled by the characteristic speed. This dimensionless measure of gene flow asymmetry can be either positive or negative, determining the direction and magnitude of upstream distortion in the evolutionary averaging kernel. The averaging distance expands upstream to $L(\sqrt{1+\varphi^2} + |\varphi|)$, and contracts downstream to $L(\sqrt{1+\varphi^2} - |\varphi|)$ (Slatkin 1978, Filin 2007; Appendix). The total geographic extent of evolutionary averaging also widens, from $2L$ to $2L\sqrt{1+\varphi^2}$, further precluding local adaptation and geographic differentiation (compare with the single-locus cline model of May et al. 1975).

A third point of symmetry between velocity of environmental change, u_θ, and advective dispersal, u, is in spatial population density profiles during invasion. As Fig. 1C shows, climate change induces high population density close to the downstream edge of the expanding range, while advective dispersal is associated with highest densities near the upstream edge (compare with the purely demographic model of Berestycki et al. 2009). In either case, maximum population density is closer to the range's edges than to its center. However, when advective dispersal matches the velocity of climate change, $u = u_\theta$, symmetrically centered density profiles are regained (not shown).

Finally, trait-dependent habitat choice is simultaneously a form advective dispersal (Eq.[4] and Eq.[5]) and a form of spatial sorting (Shine et al. 2011, Phillips & Perkins 2019). Individuals within each local population disperse at varying rates and in different directions towards environments that better match their trait value. Intuitively, therefore, one expects such matching habitat choice (Edelaar et al. 2008) to reduce local maladaptation, matching mean trait values of populations to local optima and enhancing phenotypic differentiation across space. The characteristic length accordingly shrinks to $L = \sqrt{D/[s(G + \chi b^2)]}$, and the characteristic speed accelerates to $c_g = 2\sqrt{D[s(G + \chi b^2)]}$ (Filin 2007; Appendix). Shorter characteristic lengths translate to better tracking of spatially varying selection by local

populations.

A shorter characteristic length also translates to faster invasions (Q is decreased in Eq.[7]), as supported by numerical solutions (Fig. 1G,H). Higher characteristic speeds, similarly, decrease the upstream pull of gene swamping (φ is smaller; Eq.[8]). The averaging kernel is more symmetric and equilibrium levels of maladaption are lower (given now by $a = (u_\theta - u)b/(sG + s\chi b^2)$; compare with Eq.[6]), enhancing overall persistence of the species in the environmental gradient (Fig. 1J). These expressions for characteristic length and speed and adaptation lag, under trait-dependent habitat choice, clearly demonstrate that, in eco-evo context, the role of such matching habitat choice, or spatial sorting, is equivalent to that of additive genetic variance, in promoting local adaptation. The effect manifests itself, though, only in moderate to steep environmental gradients (Fig. 1G,H,J), as it is proportional to b^2.

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Discussion

A decade ago, Sorte (2013) discussed unique challenges of climate change to advective (flow) environments and to the species that depend on them, such as marine fishes and invertebrates, wind-dispersed plants, and lotic systems (Müller 1982, Nathan et al. 2011, Bertola et al. 2020). Sorte identified the direction of flow, either upstream or downstream, relative to the velocity of climate change, as a key parameter in the future persistence of such populations. In this study, I have quantified this argument, through dependence of maladaptation, invasion speeds and spatial abundance profiles on the velocity difference, $u - u_\theta$.

Population genetics often deals with questions of adaptation and persistence in terms of loads (Barton 2024), i.e., negative effects on fitness — genetic load (Crow & Kimura 1963), lag load (Lande & Shannon 1996, Polechová et al. 2009), expansion load (Peischl et al. 2013), and so on. However, in a spatial context, where dispersal influences a multitude of coupled demographic and evolutionary processes (mixing, swamping, sorting, etc.), there is value in looking at characteristic lengths and velocities as well. This approach has been productive in demographic models of spatial spread, of averaging and tracking of environmental heterogeneity, and of population persistence (Roughgarden 1974, Shigesada et al. 1986, Shigesada & Kawasaki 1997, Speirs & Gurney 2001, Potapov & Lewis 2004, Anderson et al. 2005, Berestycki et al. 2009, Nisbet et al. 2010), and, more recently, in experimental microbial models for range expansion and invasion dynamics (Gandhi et al. 2016, Deforet et al. 2017, Birzu et al. 2019). The characteristic length has also featured prominently in models of sexual selection and geographic variation in female mating preference (Lande 1982b, Day 2000), and in studies of allele-frequency clines (Slatkin 1973, May et al. 1975, Slatkin 1978, Nagylaki 1978, Barton 1999). Wave speeds have, similarly, been studied for selective sweeps (Fisher 1937, Barton et al. 2013) and evolutionary rescue (Kirkpatrick & Peischl 2013).

That is the second symmetry that I have identified in this study. Namely, the dynamics of tracking and averaging (Roughgarden 1974, Anderson et al. 2005) of environmental heterogeneity in both demographic and evolutionary dynamics, albeit with different

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characteristic length and speed scales. A more solid appreciation of this symmetry in coupled eco-evo tracking and averaging, of transitions between the two modes, and of their modulation by gene swamping, and other eco-evo processes, should be sought.

Moreover, by identifying characteristic times, lengths and velocities, it is possible to make educated guesses about how additional processes and mechanisms may influence eco-evo dynamics, without initially having to solve complex models. Here, I demonstrated that through the added effect of matching habitat choice on characteristic length and speed. The enhancement of population densities and invasion wave speeds in advective environments (Fig. 1G,H,J) suggests a complementary mechanism for the resolution of the so-called drift paradox, on top of sufficiently high random dispersal (Speirs & Gurney 2001, Nisbet et al. 2010, Vasilyeva & Lutscher 2012).

Characteristic lengths, speeds and times additionally allow for recasting problems in terms of dimensionless ratios. This has value beyond simplifying the analytical or numerical solution of particular models, as it facilitates the use of *dimensional analysis* in interpretation of data and design of micro- and mesocosm experiments. Dimensional analysis has been applied successfully in engineering, geography, and many other scientific fields for decades. Although there has been some discussion and application (Petersen & Hastings 2001, Petersen & Englund 2005, Simpson et al. 2008, Nisbet et al. 2010, Legendre & Legendre 2012), it remains largely underutilized in ecology. By identifying a set of dimensionless ratios (such as φ and Q in this study; Eq.[7] and Eq.[8]) and a set of relationships among them, obtained from theory or empirically, one can quickly make educated guesses, without solving any sophisticated and complex models, about how a system should respond under different scenarios, beyond those directly examined. For example, the adaptation lag, Eq.[6], can be recast as $(a/\sqrt{G}) \propto \varphi Q$, a relationship that combines three dimensionless quantities, where local maladaptaion is now measured in additive genetic standard deviations, $\sqrt{G}$. This allows for quick educated guesses of how local maladaptation (or biotic lag; Lovell et al. 2023) may change under different scenarios, such as increased velocity of climate change, advective flow poleward or equatorward, or different demographic dynamics that may influence the strength of gene

swamping, φ. Dimensional analysis may also facilitate comparisons of different systems, species, populations, traits and locales, complementary to those obtained by multidimensional scaling and other multivariate statistical techniques.

Recent microcosm experiments with swarming microbes have highlighted the distinction between pulled and pushed invasion wave fronts (Gandhi et al. 2016, Deforet et al. 2017, Birzu et al. 2019, Erm & Phillips 2020). Pushed waves can occur, if the invasion front experiences an Allee effect. Pulled waves are the classic invasion fronts obtained by random dispersal and negatively density-dependent growth (e.g., logistic; Shigesada & Kawasaki 1997, Murray 2002). In here, I additionally identified an opposite pulling, due to the eco-evo coupling of demography and evolution, mediated by asymmetric gene flow (May et al. 1975, Nagylaki 1978, Filin 2007), i.e., gene swamping (Lenormand 2002). In homogeneous environments, advective dispersal simply adds to the invasion speed. But when a species needs to continuously adapt to an environmental gradient in order to invade, advective dispersal intensifies the upstream pulling of gene swamping, countering the downstream pulling by dispersal and density-independent population growth at the advancing front. This slows down the evolutionary speed of species invasion (García-Ramos & Rodriguez 2002, Filin et al. 2008). In the extreme case of steep enough environmental gradients, the invasion front changes direction, and the entire range gradually, and counter-intuitively, shifts upstream.

With climate change, the effect is reversed. Pinned ranges shift downstream in the same direction as the velocity of climate change (Pease et al. 1989, Polechová et al. 2009). With both advective dispersal, u, and climate change, u_θ, dynamics depends on the relative velocity, $u - u_\theta$. (Eq.[6], Eq.[7], Fig. 1E,F). Front reversals have been identified also by Potapov & Lewis (2004), in a demographic model of two-competing species, under climate change. This symmetry between advective dispersal and climate change, suggests some interesting directions for space-for-time substitution studies (Lovell et al. 2023). For example, by studying advective environments and the organisms that historically adapted to them as models for current and future responses to climate change elsewhere.

Gene swamping has fallen out of favor as an explanation for range limits, on both theoretical

grounds (Barton 2001, Filin 2007, Polechová et al. 2009, Matz et al. 2018), and due to lack of empirical support (Angert et al. 2020, Kottler et al. 2021). (But see, recently, Hancock et al. 2024). With the identification of a multitude of other eco-evo processes (gene surfing, expansion load, spatial sorting, etc.), gene swamping has been almost forgotten, to the point that a recent review does not even mention the term (Miller et al. 2020; cf. Lenormand 2002). In addition to causing swamping, gene flow also inflates the additive genetic variance of local populations (Slatkin 1978, Barton 2001), thus, enhancing local adaptation. In such cases, (deterministic) eco-evo models predict unlimited ranges at equilibrium (Barton 2001, Filin 2007). However, equilibrium may take a long time to achieve and, in an increasingly disturbed natural world, may be irrelevant altogether. Gene swamping is an inherent component of dispersal and gene flow in heterogeneous environments (Eq.[10] and Eq.[11]; also Bertola et al. 2020, Hancock et al. 2024). As I have shown in this study, it has important influences on evolutionary invasion dynamics (García-Ramos & Rodriguez 2002, Filin 2007, Filin et al. 2008), particularly in cases of directional flow, advective dispersal and environmental change.

Stochasticity is expected to influence invasion dynamics and range expansion. For example, Polechová (2018) on effects of genetic drift, and Birzu et al. (2018) on fluctuations in invasion fronts. The latter study, in fact, derives a gene swamping expression in their analysis, although they do not use the term, or acknowledge links to the literature on gene swamping. Therefore, stochasticity will likely modulate the strength of the pulling by gene swamping and the occurrence of invasion front reversals in eco-evo dynamics with advective dispersal. A topic for future investigation.

In summary, the symmetry between velocity of advective dispersal and flow and the velocity of climate change (Speirs & Gurney 2001, Potapov & Lewis 2004, Berestycki et al. 2009, Nisbet et al. 2010) leads to unique challenges to species persistence in advective environments under environmental change (Sorte 2013). Here, however, I additionally suggest that, because of this symmetry, populations that have historically adapted under conditions of directional flow can function as models for persistence and adaptation under climate change, in general. Such populations and species may also be preadapted to better cope with climate change, as

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the eco-evo effects of advective flow are already integrated into their life-history (Müller 1982). A second symmetry, identified here, is in the tracking and averaging of environmental heterogeneity, in both demographic and evolutionary dynamics, but with different characteristic length and speed scales. By applying dimensional analysis, a better understanding of eco-evo coupling, through such length and velocity scales, can be translated into simple dimensionless metrics, to inform micro- and mesocosm experiments (Petersen & Hastings 2001, Petersen & Englund 2005, Simpson et al. 2008, Gandhi et al. 2016), space-for-time substitutions (Lovell et al. 2023), and comparisons of different populations, species, traits and locales. A systematic application of dimensional analysis in theoretical and empirical eco-evo and climate change studies has potential to provide complementary tools and insights to those of multivariate statistics.

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Appendix

Following Filin (2007), dynamics of spatially-varying population density and trait frequency distribution (probability density function) are given by

$$\frac{\partial n}{\partial t} = \boldsymbol{\nabla} \cdot \left[\boldsymbol{\nabla}\left(\bar{D}n\right) - \bar{\boldsymbol{u}}n\right] + \bar{W}n \qquad [9]$$

$$\begin{aligned}\frac{\partial f}{\partial t} = &\left[(W - \bar{W}) + \frac{1}{n}\boldsymbol{\nabla} \cdot \left(\boldsymbol{\nabla}\left((D - \bar{D})n\right) - (\boldsymbol{u} - \bar{\boldsymbol{u}})n\right)\right] f \\ &+ D\nabla^2 f + \mu\frac{\partial^2 f}{\partial z^2} + 2D\boldsymbol{\Phi} \cdot \boldsymbol{\nabla} f\end{aligned} \qquad [10]$$

where D is a diffusion coefficient, representing random symmetric dispersal, $\boldsymbol{u}$ is a velocity vector that represents the advective (directional) component of dispersal, $\bar{D}$ and $\bar{\boldsymbol{u}}$ are their mean in the local population. Generally, both random dispersal and dispersal bias are functions of phenotype or trait, z, as well as of time, t, spatial location, $\boldsymbol{x}$, and population density, n. Though below I only consider very specific simpler forms. The operator $\boldsymbol{\nabla}$ represents spatial derivatives, i.e., with respect to spatial position $\boldsymbol{x}$. In this context, this operator defines how spatial variation in net flows of random and advective dispersal add to local population growth, given by trait-dependent fitness, W, or its population mean $\bar{W}$.

The first RHS term of Eq.[10] demonstrates the equivalence of relative fitness and relative differences in trait-dependent dispersal rates ($D - \bar{D}$ and $\boldsymbol{u} - \bar{\boldsymbol{u}}$). In Filin (2007), I called it "generalized relative fitness", which takes into account also differences in dispersal ability among phenotypes. Nowadays, it is known as spatial sorting (Shine et al. 2011). The second term is a diffusion term — the homogenizing mixing effect of random dispersal. The third term is diffusion in trait space (rather than geographic space; Kimura 1964, 1965), usually representing random mutation, but can also capture other local processes that generate trait variance, at an overall rate μ.

The fourth, and final RHS term of Eq.[10] models the effect of gene swamping. The vector $\boldsymbol{\Phi}$ captures the equivalence of spatial gradients in relative population density, spatial gradients in random dispersal rates and the directional advective dispersal,

$$\boldsymbol{\Phi} = \frac{\boldsymbol{\nabla} n}{n} + \frac{\boldsymbol{\nabla} D}{D} - \frac{\boldsymbol{u}}{2D} = \boldsymbol{\nabla}(\ln(Dn)) - \frac{\boldsymbol{u}}{2D}. \qquad [11]$$

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This equivalence has been previously shown by Fife (1979) and Nagylaki (1989) in allele-frequency cline models, and by Gurney & Nisbet (1975) in a purely demographic model.

Next, I simplify the dynamics by assuming no explicit time-dependence of parameters, except for $\theta = \theta(\boldsymbol{x}, t)$. Moreover, I will not consider the dynamics of trait variance, assuming fixed phenotypic and additive genetic variances, P and G. The dynamics of local mean trait value is given by $\dot{\bar{z}} = \int z \dot{f} dz$, where $\dot{f}$ is given by Eq.[10]. With the extra assumptions listed in Methods, and replacing the relative fitness term, $\int z(W - \bar{W}) f dz$, with the weak selection approximation of Lande (1976), $G\, \partial \bar{W} / \partial \bar{z} = -sG(\bar{z} - \theta)$, Eq.[2] follows readily. For the demographic dynamics (Eq.[1]) the genetic load term, $\frac{1}{2}sP$, in the average fitness, $\bar{W}$, has been subsumed into the definition of r and carrying capacity, as in, for example, García-Ramos & Rodriguez (2002).

When trait-dependent habitat choice is added to the dynamics of $\bar{z}$ (or a), there are extra $u - \bar{u}$ and $\bar{u}$ terms (Eq.[4] and Eq.[5] in Methods) in the general dynamics equations, Eq.[9] and Eq.[10], on top of the fixed advection velocity already considered. These terms add up to the following extra expression in the dynamics equation of mean trait, $-\int \left[\frac{\boldsymbol{\nabla} n}{n} \cdot (v - \bar{v}) + \boldsymbol{\nabla} \cdot (v - \bar{v})\right] z f dz - \int (z \boldsymbol{v} \cdot \boldsymbol{\nabla} f)\, dz$, where $\boldsymbol{v} = \chi s(z - \theta) \boldsymbol{\nabla} \theta$, $\bar{\boldsymbol{v}} = \chi s(\bar{z} - \theta) \boldsymbol{\nabla} \theta$, and $\boldsymbol{v} - \bar{\boldsymbol{v}} = \chi s(z - \bar{z}) \boldsymbol{\nabla} \theta$ (Filin 2007). Recalling that f is normal with mean $\bar{z}$ and fixed variance P, these extra terms eventually evaluate to give the following dynamics for mean trait (Filin 2007),

$$\begin{aligned} \frac{\partial \bar{z}}{\partial t} &= D \nabla^2 \bar{z} - s(G + \chi \boldsymbol{\nabla} \bar{z} \cdot \boldsymbol{\nabla} \theta)(\bar{z} - \theta) + 2D \boldsymbol{\Phi} \cdot \boldsymbol{\nabla} \bar{z} \\ &\quad - \chi s P \left(\frac{\boldsymbol{\nabla} n}{n} \cdot \boldsymbol{\nabla} \theta + \nabla^2 \theta \right) - \chi s \boldsymbol{\nabla} \theta \cdot \boldsymbol{\nabla} P. \end{aligned} \qquad [12]$$

Here, $\boldsymbol{\Phi} = \boldsymbol{\nabla} \ln(n) - \boldsymbol{u}/2D$, $\boldsymbol{u}$ being the fixed (trait-independent) advective dispersal component. Because P is fixed, the last term in Eq.[12] can be dropped. (Filin 2007 considered also the dynamics of trait variance.) Further assuming a linear environmental gradient, with slope b, one-dimensional space (dropping the vector notation), etc., I finally obtain the dynamics equation for (mal)adaptation, $a(x, t) = \bar{z} - \theta$, with trait-based habitat

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choice,

$$\frac{\partial a}{\partial t} = D\nabla^2 a - s(G + \chi b^2 + \chi b \nabla a)a + b u_\theta + 2(b + \nabla a) D\Phi - \chi s P b \nabla \ln(n), \qquad [13]$$

which demonstrates the equivalence of the term χb^2 and additive genetic variance, G, in the restoring force, due to selection, $-s(G + \ldots)a$ (compare with Eq.[2]). In other words, phenotypic sorting as equivalent to selection (Phillips & Perkins 2019). Moreover, the first two RHS terms of Eq.[13] define (to first-order, i.e., dropping the $a\nabla a$ term) characteristic length, $L = \sqrt{D/[s(G + \chi b^2)]}$, and speed, $c_g = 2\sqrt{Ds(G + \chi b^2)}$.

The demographic equation under trait-dependent matching habitat choice is

$$\frac{\partial n}{\partial t} = D\nabla^2 n - u\nabla n + \left[r(1-n) - \frac{1}{2} s a^2 \right] n - \chi s b (a \nabla n + n \nabla a). \qquad [14]$$

(Compare with Eq.[1].)

THE EVOLUTIONARY AVERAGING KERNEL. In constant environments, $\theta = \theta(\boldsymbol{x})$ or $u_\theta = 0$, and recalling that by definition $\bar{z}(\boldsymbol{x}) = \theta(\boldsymbol{x}) + a(\boldsymbol{x})$, one can obtain from Eq.[2] an expression for the mean phenotype at equilibrium,

$$\left(1 - 2L^2 \boldsymbol{\Phi} \cdot \boldsymbol{\nabla} - L^2 \nabla^2\right) \bar{z}(\boldsymbol{x}) = \theta(\boldsymbol{x}). \qquad [15]$$

Dropping the vector notation for the one-dimensional case ($\boldsymbol{x} = x$), it is straightforward to show, by Fourier transform, that this expression defines an averaging scheme over $\theta(x)$, or low-pass filter (Slatkin 1978, Filin 2007). The averaging kernel is given by two separate decaying exponentials for positive and negative distances from the focal locality, x of $\bar{z}(x)$, corresponding to downstream and upstream directions,

$$h(\xi) = \frac{1}{\alpha L + L/\alpha} \begin{cases} e^{-\frac{\xi}{L/\alpha}} & \text{when } \xi > 0, \\ e^{+\frac{\xi}{\alpha L}} & \text{when } \xi \leq 0. \end{cases} \qquad [16]$$

The parameter α represents the contraction downstream and expansion upstream of the averaging kernel, due to asymmetric gene flow, $\alpha = \sqrt{1 + \varphi^2} + \varphi$, where $\varphi = L\Phi$. The mean phenotype at equilibrium is then given by $\bar{z}(x) = \int \theta(x + \xi) h(\xi) d\xi$, a low-pass-filtered optimum.

With climate change, $u_\theta > 0$, a transformation of the space variable x to $x - u_\theta t$ restores a constant (time-invariant) environmental gradient. In this case, Φ (Eq.[3]) includes advection velocity of $u - u_\theta$, which leads to φ according to Eq.[8].

APPROXIMATE EXPRESSION FOR INVASION SPEED. Under a change of space variable, $y = x - ct$, I look at a traveling wave solution of the form $n = n_0 e^{-\kappa y}$ and $a = a_0 - qy$, $q, \kappa > 0$, for large y, i.e., at the advancing front, where population density is low, and growth is thus approximately density-independent. Substitution into Eq.[1] and Eq.[2] yields $\kappa = \frac{(c-u)\pm\sqrt{\Delta}}{2D}$, where the discriminant, Δ, is given by $\Delta = (c-u)^2 - 4D(r - \frac{1}{2}a_0^2)$. The expression for baseline maladaptation, a_0, is $a_0 = b(u_\theta - c)/sG$. Substituting into the equation for the discriminant and setting $\Delta = 0$ (Shigesada & Kawasaki 1997, Murray 2002) finally yields Eq.[7] for invasion speed, c.

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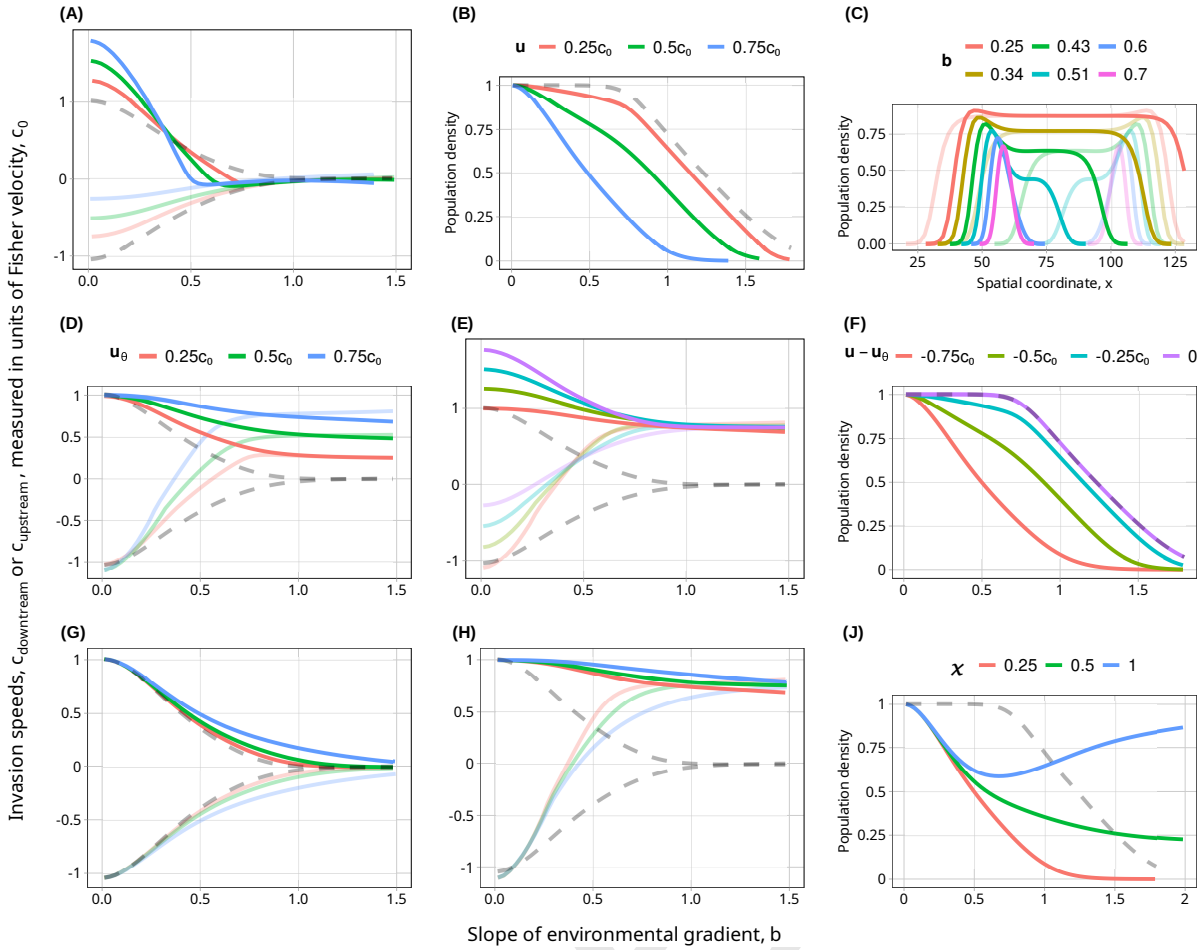

Figure 1 : Invasion speeds of both downstream (solid lines) and upstream (transparent lines) wave fronts and population densities, as functions of slope of environmental gradient, b (except C). As the velocity of advective dispersal, u, increases (A; legend in B), invasion speeds shift downstream. Dashed line represents the case of no advective dispersal and no climate change ($u = u_\theta = 0$), i.e., purely symmetric random dispersal in a constant environmental gradient (invasion speeds in this case are in agreement with Figure 6 of Filin et al. 2008 for genetic variance parameter $A = 0.5$ and logistic density-dependence). Clearly, for the purely demographic case ($b = 0$), $c = c_0 + u$, as expected (Shigesada & Kawasaki 1997). For steeper gradients, invasion speeds decline in both downstream and upstream fronts (as expected for evolutionary speeds of invasion; García-Ramos & Rodriguez 2002). Range pinning, where curves of downstream and upstream velocities converge, occurs at increasingly shallower gradients (lower values of b), as advective dispersal, u, increases. Final maximum population density (B) also decreases with both steepness of environmental gradient, b and velocity of advective dispersal, u. Filin (2007), in fact, derived a condition for persistence in the environmental gradient $b < b_U \propto \left(1 - \frac{u^2}{c_0^2}\right)$ (cf. Speirs & Gurney 2001, Potapov & Lewis 2004, Nisbet et al. 2010, in purely demographic scenarios of advective flow). For velocity of climate change, u_θ, effects are overall similar (D), though in this case, invasion speeds decline towards u_θ, not 0 (compare to A). The symmetry is also evident when comparing spatial abundance profiles (C). Profiles for $u = 0.5c_0$ (solid lines) and profiles for $u_\theta = 0.5c_0$ (transparent lines) are mirror images of each other, around the midpoint of initial introduction. Thus, with advective dispersal, densities shift upstream, due to pulling by gene swamping. With velocity of climate change they are higher downstream (cf. Berestycki et al. 2009), towards shifting environments priorly adapted to. Such non-abundant-center density profiles suggest that, in eco-evo scenarios, even without stochasticity, nonequilibrium processes, in this case, ongoing spatial spread and (mal)adaptation, produce maximal densities closer to range margins (cf. Faurby & Araújo 2018, Dallas et al. 2020). With both advective dispersal and climate change (E; legend in F), dynamics depends on the velocity difference $u - u_\theta$. When u matches u_θ, one clearly regains the symmetric random dispersal case (dashed line), only shifted downstream by u_θ (here $u_\theta = 0.75c_0$). Symmetry is also evident in final maximum densities (F; compare with B). Finally, G, H, J (common legend in J) demonstrate the added effect of matching habitat choice, through the parameter χ. Clearly, population density (persistence) is enhanced, invasion speeds are higher (Filin 2007), and range pinning requires steeper environmental gradients, as habitat choice gets stronger (cf. Pellerin et al. 2019). $u = u_\theta = 0$ in G. $u_\theta = 0.75c_0$ in H, J (compare with D).